

Feeding behaviours of neotropical butterflies (Lepidoptera, Papilionoidea)

Ingestión de alimentos en mariposas neotropicales (Lepidóptera, Papilionoidea)

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Abstract: The rainforest surrounding the Estación tropical La Gamba in the Piedras Blancas National Park contains a rich butterfly fauna. Corresponding to this high biodiversity are the many examples of specialised feeding preferences of the adult butterflies. The majority of them visit flowers and feed on nectar, but many species are also attracted to fluids containing mineral substances. They can be observed to feed on sweat, urine or moist soil. Additionally, some nectar-feeding nymphalid butterflies extract pollen and others collect alkaloids from certain plants. Furthermore, there is a rich fauna of obligatory non-nectar feeding nymphalids. Among the latter are butterflies which have been observed to feed exclusively on fermenting fruit, tree sap, dung or other rotting substances. The specialised feeding preferences are reflected in modified feeding behaviour and mouthpart morphology which is adapted to the particular feeding ecology.

Key words: feeding behaviour, mouthparts, butterflies, insects.

Resumen: El bosque cerca de la Estación tropical La Gamba en el Parque Nacional de Piedras Blancas contiene una fauna rica en mariposas. La gran diversidad de estos insectos se refleja en sus muy variados requisitos alimenticios. Además de néctar floral, muchas mariposas necesitan líquidos ricos en minerales, por eso pueden ser observados ingiriendo sudor, orina o agua pantanosa. Además existen especialistas alimentarios que utilizan adicionalmente extracto de polen y de hojas como alimento, o que toman exclusivamente jugos de frutas y de árbol fermentados y que succionan líquidos de los excrementos.

Palabras clave: ingestión de alimentos, aparato bucal, mariposas, insectos.

Introduction

All butterflies possess a long and very flexible proboscis to imbibe liquid foods by suction. The organ is coiled up and stored under the head during rest; to feed, it uncoils in a split second by an increase in blood pressure (KRENN 1990). The proboscis consists of two half pipes which form a central food canal that functions like a drinking straw through which liquids are sucked from the organ's tip into the head and finally the digestive tract. A pump located in the head produces the necessary pressure gradient to transport liquids into the oesophagus (EBERHARD & KRENN 2005). Liquid foods enter the proboscis through a row of small slit-like openings at the tip (PAULUS & KRENN 1996, KRENN 1998). Although the mouthparts of all butterflies are similarly composed, different food preferences exist, and various feeding guilds can be distinguished which have been relatively well investigated in neotropical butterflies (e.g. PINHEIRO & ORTIZ 1992, DEVRIES et al. 1997, KRENN et al. 2001).

Floral nectar is the most common type of food for butterflies in general, and this holds true for the fauna of Costa Rica (DEVRIES 1983). Flowering plants that are generally visited by butterflies secrete a nectar that is richer in amino acids than plants which are pollinated by other insects (BAKER & BAKER 1973). The supply of amino acids is the deciding factor for one feeding guild – the nectar- and pollen-feeding passionvine butterflies which are exclusive to the neotropical region. There is also an amazing series of nymphalid butterflies which never visit flowers, instead obtaining liquids from rotting fruit, dung, carrion and fungi. Many species of butterflies have extremely specialised feeding preferences; for example, several species have so far only shown an attraction to dog faeces (DEVRIES 1983). Many butterflies from all feeding guilds are attracted to moist soil which is often wetted by urine. These are predominantly male butterflies seeking sodium and albumin, presumably to increase their reproductive success (DOWNES 1973, ARMS et al. 1974, BECK et al. 1999).

This chapter summarises the feeding behaviour involving different sources of food for butterflies occurring at the Estación tropical La Gamba and the Esquinas rainforest of the Piedras Blancas National Park (Costa Rica). Movements and positions of the proboscis differ among the members of the various feeding guilds. These differences are reflected in the morphology of the proboscis and can be interpreted as adaptations to the peculiarities of the preferred types of food.

Material and Methods

Starting with a list of butterflies from the Estación tropical La Gamba (KEBER 1997), an evaluation of the data on their feeding preferences was conducted on the various species (DEVRIES 1983, 1987, 1997). Feeding behaviour on different sources of food was observed and analyzed for several representatives of the Nymphalidae. Observations and video recordings were made in the Estación tropical La Gamba and the surrounding Esquinas rainforest of the Piedras Blancas National Park during August 2004 and February 2007 using a Sony TRV 740 ES digital video camera. In addition, unpublished video recordings were consulted which were taken under near-natural conditions in a glasshouse of the Department of Zoology of the University of Texas at Austin, in September 1995.

The behaviour of the butterflies during floral nectar feeding was observed on inflorescences of *Lantana camara* (Verbenaceae). The flowers of this very common neotropical plant were frequently visited by butterflies. Movements of the proboscis were analysed and the time required to exploit individual flowers was recorded for the various species. A total of 6 butterfly species – *Anartia fatima* (n = 17), *Agraulis vanillae* (n = 8), *Dryas julia* (n = 5), *Heliconius erato* (n = 13), *H. hecale* (n = 15), and *H. charitonia* (n = 3) – were examined under natural conditions and in the glasshouse. Flower handling times of 34 feeding events were compared for each species. Pollen-collecting behaviour on flowers of *Psiguria tabascensis* (Cucurbitaceae) was filmed and analysed for *Heliconius erato* (n = 10) and *H. hecale* (n = 7). The flowers of the neotropical gourd genus *Psiguria* are often visited by pollen-collecting species of *Heliconius*-species (MURAWSKI & GILBERT 1986, ESTRADA & JIGGINS 2002). The analyses from the glasshouse were supplemented by field observations of *H. hecale* when feeding on *Psychotricha elata* (Rubiaceae) in the Esquinas rainforest in February 2007.

The behaviour of non-flower-visiting butterflies, such as *Baeotus baeotus* (Nymphalinae), *Hamadryas amphinome* (Nymphalinae), *Eunica alcmena* (Nymphalinae), *Temenis laothoe* (Nymphalinae), *Diaethria astala*

(Nymphalinae) and *Megeuptychia antonoe* (Satyrinae), was filmed on banana bait in the Estación tropical La Gamba. Video recordings of *Morpho peleides* (Morphinae) feeding on rotting bananas and moistened surfaces, which were taken in a glasshouse at the University of Vienna (KNOPP 2001), were also analysed. The digital recordings of the movements of the proboscis and the measurements of the duration of the movements were analyzed with the aid of the computer program "Observer" at the Department for Evolutionary Biology of the University of Vienna.

Results

Diversity of feeding behaviour

The list of butterflies in Estación tropical La Gamba and the surrounding forests of the Piedras Blancas National Park includes more than 120 identified species (KEBER 1997, personal observation). Statements on their food preferences can be made for 93 of these species (DEVRIES 1987, 1997, KEBER 1997, personal observation). Accordingly, 61 butterfly species are considered to be flower visitors, fulfilling the essential part of their nutritional demands by feeding on nectar from various flowers. Approximately 30 species are never found at flowers, but nourish themselves predominantly from rotting fruit, tree sap, honeydew and fungi, but also carrion and fresh excrement. Some species appear to utilise all kinds of food sources (DEVRIES 1987). As with most butterflies, it is usually the males who additionally probe moist ground or puddles and suck up the mineral-rich liquids.

As far as observations permit, it is safe to say that all representatives of the Papilionidae, Pieridae, Riodinidae and Hesperidae are nectar-feeding flower visitors. Regarding the food preferences of the Lycaenidae, only a few statements are available, but these also indicate that nectar is the main food source (KEBER 1997). A great variety of food preferences is exhibited among the Nymphalidae. Of the 75 species of Nymphalidae in the Estación tropical La Gamba and surroundings, for which statements on food sources exist, 42 are nectar-feeding flower visitors. Of those, nine *Heliconius* species and *Laparus doris* additionally collect pollen; nine species of the genera *Adelpha*, *Doxocopa* and *Marpesia*, as well as *Siproeta stelenes* also additionally suck on rotting fruit and other decaying substances, and the males of Ithomiinae, e.g. *Mechanitis polymnia* apparently also collect pyrrolizidine alkaloids from wilted leaves of certain plants. In the feeding guild that does not visit flowers, 33 species from the family Nymphalidae feed exclusively on rotting fruit and fungi, tree sap, fresh mammal manure and carrion. Until now, some of these species have



Figs. 1-3: Nectar-feeding nymphalid butterflies on inflorescences of *Lantana camara* (Verbenaceae). **(1)** *Dryas julia* (Heliconiinae) probes single flowers of *Lantana camara* by turning movements of the body. Arrow indicates movements of the distal region of the proboscis. **(2)** *Anartia fatima* (Nymphalinae). Proboscis in flexed position during probing behaviour. The arrow indicates the vertical movements of the proboscis. **(3)** *Anartia fatima* (Nymphalinae). Proboscis completely introduced into a single floret during nectar uptake.

only been observed imbibing liquids on moist sand; whether these species additionally visit other food sources is not known.

The following descriptions of the behaviours and movement patterns of feeding on different food sources refer to different species of the Nymphalidae occurring in Estación tropical La Gamba and surrounding forests, but basically also apply to butterflies of other neotropical regions.

Flower-visitors and nectar feeding behaviour

All regular flower-visiting butterflies are nectar feeders. They perform similar flower-visiting behaviour, and the probing movements of the proboscis show a characteristic pattern which can be especially well observed when they feed on nectar from inflorescences. The pattern of behaviour can be most easily examined and compared at inflorescences of *Lantana camara* (Verbenaceae) (Figs. 1-3), since these plants are frequently visited by many different butterflies and offer ample amounts of nectar, such that longer visits to the flowers are guaranteed. KEBER (1997) listed 35 species at inflorescences of *Lantana camara* in the surroundings of the La Gamba station. In all observed species, the same basic pattern of probing and tactile movements could be recognised, and similar positions of the proboscis occur during nectar feeding. Differences were evident due to the different lengths and proportions of the proboscis in the various species.

A butterfly usually approaches an inflorescence with a loosely unrolled proboscis. This means that before landing on the flower, the proboscis has been released from its tightly coiled position of rest and is unwound to a few large coils. The proboscis is then flexed upward at its attachment point to the head capsule and unrolls in a

fast movement. In most cases this leads to a characteristic bending of the proboscis which occurs at approximately one third of the proboscis length, and the remaining two thirds of the proboscis are aimed downward (Figs. 1, 2). The region of the inflection of the proboscis, called the bend region, separates the proximal region of the proboscis, which is held forward, from the distal region of the proboscis which extends to the tip and points downward (Figs. 1, 2). The shape of the bend region in individual species depends on the length and the proportions of the regions of the proboscis.

The entire proboscis can be lifted and lowered at its jointed connection to the head; the bend region also functions like a joint, so that the distal proboscis can be stretched out or retracted by stronger flexion. Characteristic sequences of these movements allow the animals to probe flowers for nectar with the tip of the proboscis. The movements are usually restricted to the median body plane, and only the tip of the proboscis can be bent sideways. A characteristic sequence of movements consists of (1) elevation of the proboscis until the tip no longer touches the surface, (2) extension or flexion of the bend region which moves the tip of the proboscis forward or backward, followed by (3) a lowering of the proboscis until its tip again contacts the flower at another spot. Often the butterfly performs several short series of this probing behaviour usually lasting 0.2-0.5 seconds and consisting of 2-5 cycles, until the animal has found the tubular opening of the flower (Figs. 1, 2).

Once a butterfly has found the entrance to a flower, it lowers its proboscis at the base and introduces the distal section into the flower (Fig. 3). Depending on the length of the proboscis and depth of the corolla of the flower, the proboscis is inserted up to the bend region or even further. It can often be seen that the head bows

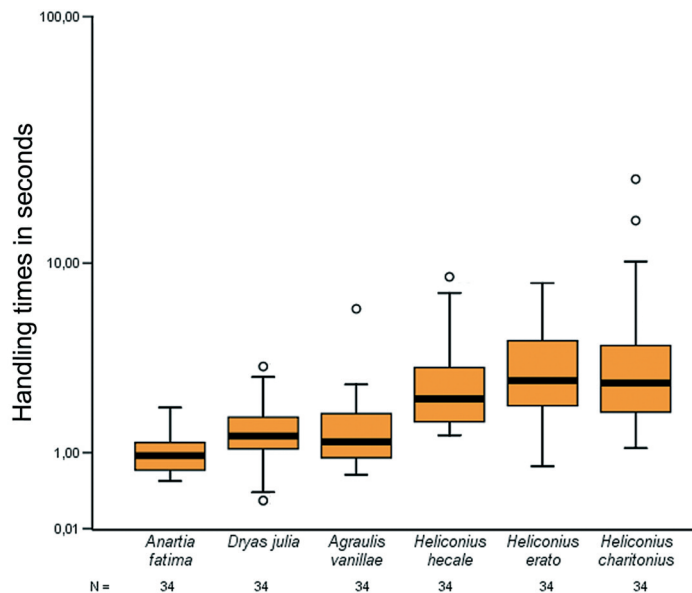


Fig. 4: Handling times of single flowers of *Lantana camara* (Verbenaceae) in various nymphalid species. The nectar-feeding species *A. fatima*, *D. julia* and *A. vanillae* are significantly faster than nectar-plus-pollen feeding *Heliconius* species (U-test, $p < 0.001$).

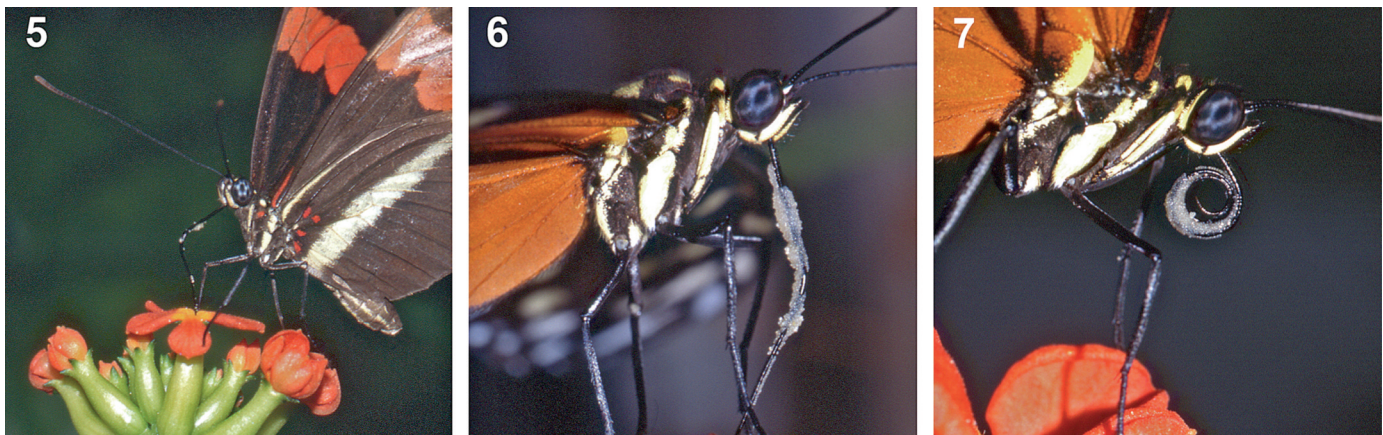
downward and the legs flex; these are movements associated with the lowering of the proboscis into the flower (Fig. 3). Butterflies often sit in the middle of an inflorescence of *Lantana camara*, and are surrounded by the numerous J-shaped corollas of the individual flowers. From one location, the butterfly can insert its proboscis successively into many individual flowers whereby the bending of the proboscis assumes the same curvature as the corolla of the flower. After the proboscis is introduced into the flower, brief poking movements often follow. In short series of 1 to 6 poking movements, the proboscis is partially lifted from the flower and immediately inserted again. Commonly, each poking movement lasts less than a second. While nectar is sucked out of the corolla tube

the proboscis is held still for only a brief moment in the flower. When the flower is depleted of nectar, the proboscis is pulled out, and the butterfly moves to the next flower, probes to find the entrance and inserts the proboscis. In this manner, a butterfly sitting in the middle of an inflorescence (Fig. 1) can swiftly exploit one flower after another by simply rotating its body.

This sequence of movements is relatively uniform, stereotypical and differs little within the examined species. Clear differences are however evident regarding the time needed to exploit individual flowers. In the nectar feeding nymphalids, the average handling time per flower ranges from 1.0 ± 0.34 seconds to 1.49 ± 1.0 seconds. The pattern of probing behaviour of the nectar- and pollen-collecting species of *Heliconius* is the same, but the entire sequence of movements is slower, even if the butterflies feed only on nectar. The flower handling times are significantly longer in *Heliconius*, measuring on average of 2.71 ± 1.61 seconds to 4.21 ± 4.3 seconds in the studied species ($p < 0.001$, U-test) (Fig. 4).

Pollen feeding behaviour

Pollen collecting behaviour of butterflies was studied on inflorescences of *Psiguria* with the help of video recordings and was compared to their behaviour on flowers of *Psychotria elata* (Rubiaceae). The probing movements of the proboscis are, in principle, identical to those previously described with *Lantana*. Once the entrance to an individual flower has been found, the butterfly inserts the proboscis (Fig. 5). This is usually accompanied by additional movements of the head, and it appears as if some resistance must be overcome. A series of relatively slow yet powerful up and down poking movements follow. Once the proboscis is completely introduced into the flower, it often remains motionless for several seconds. When the proboscis is extracted from



Figs. 5-7: Pollen feeding behaviour of *Heliconius* (Heliconiinae). (5) *H. erato* visits an inflorescence of *Psiguria tabascensis* (Cucurbitaceae). Probing behaviour with flexed proboscis is similar to nectar feeding behavior. (6) *H. hecale* collects pollen on the proboscis by repeated poking into a single flower. (7) Using saliva, *H. hecale* extracts amino acids from the pollen by uncoiling and coiling the recoiled proboscis using saliva.

the narrow corolla, pollen grains are loosened from the anthers located on the sides of the corolla and adhere to the outer surface of the proboscis (Fig. 5). Long series of probing movements of the same single flower follow in which the proboscis is inserted deeper into the flower and pulled out relatively far so that pollen adhering to the outside of the proboscis is pushed to the proximal half of the proboscis where it accumulates and gradually forms a small lump (Fig. 6). Handling time per flower is considerably long on *Psiguria tabascensis*; it is highly variable and can last up to several minutes in some cases. The handling times for individual *Psiguria* flowers ranges from 35.6 ± 71.82 seconds to 60.27 ± 102.57 seconds on average. This is significantly longer than the handling times of *Lantana* flowers of the same butterfly species (Fig. 8). Experiments with *H. hecale* at manipulated flowers of *Psiguria*, in which the stamens were removed, showed that butterflies will only persistently probe flowers which contain pollen. Flowers without pollen are probed only briefly and then abandoned. This might be the reason for the extremely high variability of the handling times of *Psiguria* flowers.

Once the butterflies have collected a sufficient amount of pollen, they begin to knead it by repeated coiling and partial uncoiling of the proboscis (Fig. 7). During this behaviour which can last for hours, a liquid, presumably saliva, is excreted from the tip of the proboscis.

Fruit feeding behaviour

Many fruit-feeding butterflies can be observed in the Esquinas rainforest (Fig. 9). The feeding behaviour was documented on rotting bananas with video recordings in the laboratory and six species in the Estación tropical La Gamba (Fig. 10).

In general, the searching and probing movements of the proboscis are very similar to that exhibited by flower

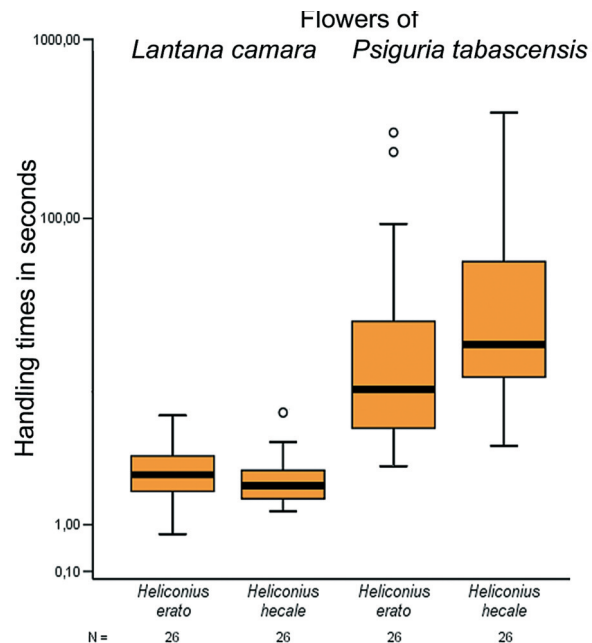
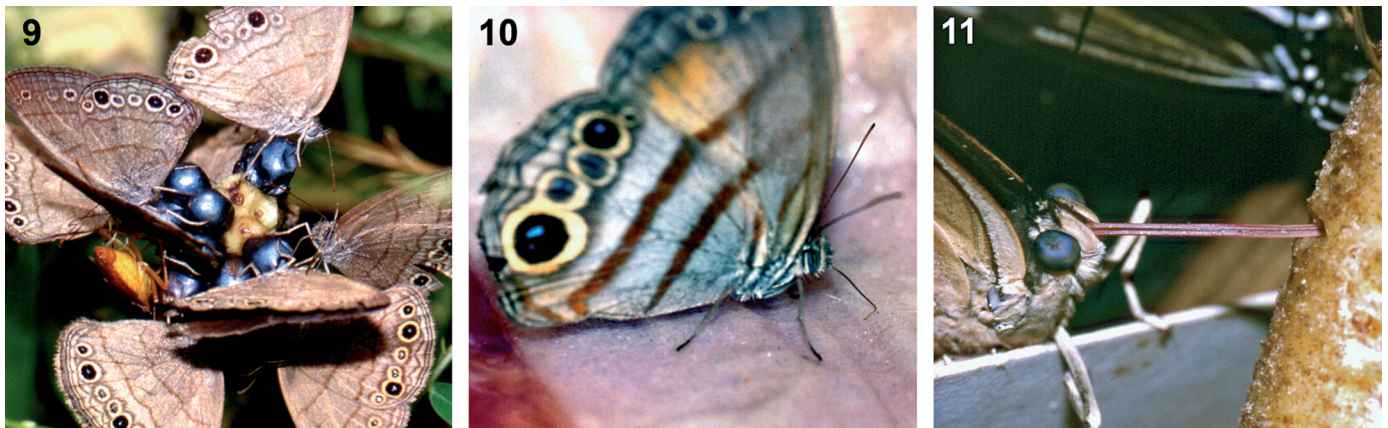


Fig. 8: Handling times of *Psiguria* flowers are significantly longer than *Lantana* flowers in *H. hecale* and *H. erato* (U-test, $p < 0.001$).

visitors. However, the proboscis of obligatory non-flower-visitors is usually relatively shorter, more brightly coloured and more flexible than in nectar feeders. When extended, the proboscis bend region is hardly recognisable (Fig. 10). The proximal section of the proboscis is only weakly curved, but the distal section is clearly curved with a relatively large radius. When extended, the tip of the proboscis is flexed that its upper side points downward. It is this characteristic position of the proboscis curving back on itself which permits the butterflies to suck liquids from a moist surface since the openings into the food tube lie on the upper side of the tip of the proboscis (Fig. 12). The searching movements consist, as before, of raising and lowering of the entire proboscis as well as back and forth movements of the distal section. In contrast to the feeding behaviour of nectar-feeding butterflies, the proboscis is often extend-



Figs. 9-11: Fruit feeding Nymphalidae. (9) *Cissia hermes* (Satyrinae) feed from ripe fruit of *Lantana camara* (Verbenaceae). (10) *Megeuptychia antonoe* (Satyrinae) sucks the moist surface of a banana bait. Short proboscis extended nearly straight, tip region flexed upside down. (11) *Archaeoprepona demophoon* (Charaxinae) pierces a rotting banana and takes up food from inside.



Figs. 12-14: Feeding from various moist surfaces. **(12)** *Morpho peleides* (Morphinae). Proboscis tip in upside-down position while feeding on honeydew from a leaf. Arrow indicates lateral movements of the proboscis. **(13)** *Marpesia* sp. (Nymphalinae) takes up mineral substances from the ground; proboscis tip in upside-down position. **(14)** *Callicore atacama* (Nymphalinae), feeds on sweat from human skin.

ed straight or bent sideways. It is thus possible for the butterfly to scan the entire substrate beneath the tarsi of the middle legs to the tips of the antennae without having to move. If the butterfly finds a favourable location to imbibe liquids, it may remain still for several minutes. The butterflies sometimes perform a particular sequence of probing movements so that the tip is not lifted completely from the surface but repeatedly returned to the same position. It could be shown that *Morpho peleides* deposits saliva to dilute the food and is thus able to dissolve and suck up dried fruit juices (KNOPP 2001) and honeydew (Fig. 12).

Compared to the rapid feeding movements of flower-visiting species, which quickly work flower after flower, the movements of non-flower-visiting species proceed at a more leisurely pace. While otherwise remaining motionless and holding the wings in the closed position, feeding behaviour of non-flower-visiting butterflies alternates between two phases of proboscis movements. In one, the butterfly performs long series of probing movements with its proboscis. In the second phase, the butterfly remains completely motionless while it sucks liquid from the moist surface. This behaviour can be described as mopping/sucking, whereby the liquid must first accumulate on the tip region of the proboscis by adhesion to sensilla before it can be drawn through the food-tube by suction.

Uptake of mineral substances and puddling behaviour

The behaviour of butterflies which feed from wet ground (Fig. 13), human sweat (Fig. 14), puddles of urine or dirty standing water, proceeds in much the same manner as outlined above. In many species the proboscis extends to a nearly straight position where only the tip region with the suction slits is bent upside-

down (Figs. 12-14). The feeding behaviour of *Temenis laothoe* was analysed as it imbibed diluted urine from the ground. The liquid was taken up over an extended period of time with dabbing movements of the uncoiled proboscis. The search movements and position of the proboscis essentially correspond to the intake of liquids from the surface of rotting fruit.

Feeding preferences

The neotropical butterfly fauna has the highest species richness in the world (DEVRIES 1987, 1997). This high biodiversity is reflected in the high diversity of adult feeding preferences and lifestyles such as nectar feeding, nectar plus pollen feeding, nectar plus alkaloid feeding, and feeding on rotten fruit, fungi, sweat, fresh mammal dung, urine or bird droppings (DEVRIES 1987). There are even reports which suspect some neotropical butterflies to feed from blood or tears (BOURGOGNE 1970, LAMAS 1986, BÜTTIKER 1997). The diversity of these food preferences is closely associated with specialisations of the mouthparts (KRENN et al. 2001), which are adaptations to the respective food preferences. Why all food specialists belong to the same family, namely the Nymphalidae remains unexplained so far. It should be noted, however, that the lifestyles of other families, such as Lycaenidae and Riodinidae, are largely unknown and it cannot be excluded that they also contain non-nectar feeding species (HALL & WILLMOTT 2000).

Floral nectar

Nectar represents the ancestral type of food for adult butterflies (KRENN et al. 2001). Of the approximately 90 species of butterflies in La Gamba, for which food preferences are known, over 60 species feed predominately on nectar from various flowers. Flower-visiting butterflies with their long and flexible sucking proboscis are able to search with great speed and precision for nectar

from diverse kinds of flowers and can suck up even minute quantities of nectar. The searching movements of the inflected proboscis together with a series of swift poking movements enable the butterflies to quickly and efficiently search for nectar with just the tip of the proboscis in flowers and inflorescences, which consist of numerous small individual flowers (KRENN 1990, 1998).

The proboscis of flower-visiting species is usually between 10 and 30 mm long and corresponds to about or $\frac{3}{4}$ of body length (PAULUS & KRENN 1996). The proboscis is only substantially longer than the body in a few butterflies. The reported record holder among true butterflies is *Eurybia lycisca* (Riodinidae), also found in the Estación tropical La Gamba, in which the extremely thin proboscis, is up to 45 mm long, twice as long as the body (BORRELL & KRENN 2006). Usually, the proboscis of a flower-visiting butterfly is slim and tapers towards the tip. The flexible tip region of the proboscis, which is equipped with suction-slits and relatively few short tactile and gustatory sensory organs, represents less than 10% of the proboscis length. The sensory structures provide information on how deep the proboscis is inserted into a flower and simultaneously whether nectar is actually present in the flower (KRENN 1998).

Pollen-collecting and extraction of amino acids

The 38 species of passionvine butterflies from the genera *Heliconius* and *Laparus* not only feed on floral nectar but also collect pollen from various flowers (GILBERT 1972, BOGGS 1981, ESTRADA & JIGGINS 2002). There are ten species of pollen-feeding butterflies in the Esquinas rainforest. In addition to nectar, these butterflies are able to utilise pollen which accumulates on the outside of the proboscis during flower visitation. The lump of pollen grains yields valuable nutrients such as amino acids by an extraction process (GILBERT 1972). In comparison to other Heliconiidae, the proboscis of pollen-feeding butterflies is longer, the proximal section exhibits conspicuously long sensilla which function to help retain pollen grains and presumably also provide information on size of the pollen-packet (KRENN & PENZ 1998). The flower-visiting behaviour of these species differs from most butterflies in the timing and duration of the search movements. *Heliconius* butterflies remain at the flowers for a much longer period of time and they poke in and out of the tubular flower openings until pollen has accumulated. Pollen grains stick to the outside of the proboscis with the help of saliva which emerges at the tip of the proboscis (PENZ & KRENN 2000). This liquid contains proteases (EBERHARD et al. 2007) and is able to extract the amino acids from the pollen (O'BRIEN et al. 2003). The pollen grains remain outside the proboscis and are themselves not ingested but drained of their nutrients. The obtained

amino acids are known to extend the lifespan of the butterflies up to 8 months. They also serve in the production of eggs or may be transferred from the male to the female during copulation. Both sexes probably rely on amino acids to synthesise substances which protect them from bird predation and pollen feeding might be the evolutionary basis of the mimicry phenomena which are common in Heliconiinae (GILBERT 1972, DUNLAP-PIANKA et al. 1977, BELTRAN et al. 2007).

Alkaloids from withered leaves

All representatives of the subfamilies Ithomiinae and Danaidae are presumed to be typical flower-visiting nectar-feeding butterflies. The males of some of these species (e.g. *Mechanitis polymnia*, a common species on the forest trails in the Piedras Blancas National Park) are known to obtain a precursor substance for the production of the male sex pheromone from particular flowers or dead and dry parts of plants (DEVRIES 1987). The male butterflies discharge a liquid from the proboscis tip region which dissolves plant materials from the wilted leaves that are then sucked up (BOPPRÉ 1983). Plants belonging to the families Boraginaceae and Asteraceae are attractive to the males since they contain pyrrolizidine alkaloids which are poisonous secondary plant substances. From these substances, the males synthesise pheromones with which they lure females during courtship display, and these substances also serve as poisonous deterrents and protect against predators (BOPPRÉ 1983).

Fruit juice and tree sap

Many tropical representatives of the family Nymphalidae never consume nectar in the course of their life, instead feeding on fruit juices, fungi or tree sap. This non-flower-visiting guild accounts for approximately 20% of the entire butterfly fauna in Costa Rica (DEVRIES 1987). The feeding behaviour and morphology of the proboscises are particularly modified. Most species obtain liquids by dabbing their proboscis from moist surfaces, while only butterflies of the subfamily Charaxinae actually pierce fruits (MOLLEMAN et al. 2005).

Fruit-piercing technique

It has been known for a long time that the African representatives of the Charaxinae are able to pierce fruits with the proboscis (NORRIS 1936). Their proboscises are comparatively short, thick and robust. The butterflies search the skin of a fruit for cracks and injuries where they can thrust in their proboscis to reach the pulp (MOLLEMAN et al. 2005). In extended position they project forward in a straight line and show no bending. The tip is clearly pointed and equipped with

only very short sensilla which do not hinder the penetration into the pulp (KRENN et al. 2001, MOLLEMAN et al. 2005). Some of the 45 species of Charaxinae in Costa Rica (DEVRIES 1987) are probably also capable of piercing and sucking on fruits, but this behaviour has so far only been documented for one neotropical species (Fig. 11) (KRENN et al. 2001).

Fruit-sweeping technique

One of the showiest butterflies is the shiny blue *Morpho peleides*, which feeds on fruit juices and tree sap (YOUNG 1975). Its proboscis is thicker than in related flower-visiting species, and remains widened even at the tip where there are long and broad suction-slits and long, numerous and densely arranged sensilla (KRENN et al. 2001, KNOPP & KRENN 2003). Behavioural experiments show that these butterflies are incapable of obtaining nectar from narrow-tubed flowers. *Morpho peleides* is, however, better able to imbibe liquids from moist surfaces than flower-visiting nymphalid butterflies. The long sensilla at the tip region of the proboscis presumably prevent penetration into the flowers. They may function like a brush on which droplets of liquid are formed by adhesion which can then be sucked into the food tube. With dabbing and sweeping movements, the proboscis scans over the moist surface and, with secreted saliva, even dried-up juice can be liquefied or thick fruit juice diluted so that it can be ingested (KNOPP & KRENN 2003).

Comparative morphological studies of the proboscis in various fruit juice feeders show that the tip region of the proboscis is, in almost all species, shaped like a brush that can measure up to one quarter of the length of the proboscis. The phylogeny of these butterflies indicates multiple independent evolution of the brush-like proboscis tip in nymphalids (KRENN et al. 2001). Behavioural observations reveal similarities. For example, when feeding, the distal end of the proboscis is positioned so that its upper side always contacts the food substrate. When the apex is positioned upside-down, the intake slits of the upper side are directed towards the substrate. Simply by raising and lowering the entire proboscis and bending the tip sideward region, these butterflies can scan a relatively wide area without having to move about. When feeding, the fruit-feeding butterflies usually close their wings, showing the camouflage pattern of the underside of their wings, making the butterflies almost invisible on the ground (KOEPEKE 1980).

Dung, carrion and decaying animal substances

Even excrement is commonly visited by butterflies, where liquid on the surface can be imbibed. Some species are particularly specialised on rotting organic material and can only be lured by foetid substances (DE-

VRIES 1987). Most butterflies which visit excrement perform dabbing movements with the proboscis similar to those of the fruit juice feeders.

One group of South American butterflies has a particular taste for bird droppings. They are the so-called ant butterflies of the genus *Mechanitis* (Ithomiinae) and also occur in La Gamba (KEBER 1997). They have repeatedly been observed to feed on the excrement of antbirds that follow the predatory marches of army ants (*Eciton* sp.) and catch the insects scared up by ants. The females of the ant butterflies often fly into the middle of a train of ants to settle on fresh bird excrement and ingest the liquid there. It is assumed that the females primarily utilise nitrogen-containing substances from the excrement, for the development of eggs (RAY & ANDREW 1980).

Feeding on perspiration or from sodium-containing liquids on the ground also requires dabbing movements of the proboscis very much like feeding from rotting fruit. All these modes of feeding presumably represent an adaptation to feeding on liquids from moist surfaces. As with fruit-juice and pollen feeders, saliva presumably plays a significant role in this derived form of food preference, but this has yet to be demonstrated. The pattern of proboscis movements in flower-visiting nectar-feeding butterflies is regarded as ancestral, while the pattern in non-flower-visitors is interpreted as derived. This derived behavioural pattern, along with a rather short proboscis equipped with a modified and elongated tip region, is found in nearly all non-flower-feeders and must have arisen independently in various phylogenetic lineages of Nymphalidae (KRENN et al. 2001).

Blood, sweat and tears

Perspiration is attractive for many butterflies and presumably serves as a source of mineral substances. It has been documented that some neotropical species of butterflies also feed on tears (LAMAS 1986, BÜTTIKER 1997). Single observations attest that Nymphalinae from the genus *Catagramma* are even able to puncture the human skin and suck blood (BOURGOGNE 1970, G. LAMAS, personal communication). However a morphological examination of the relatively short and weak proboscis of these butterflies found no indication of special characteristics or structures which could be biomechanically interpreted as useful for this behaviour, and likewise there was no resemblance to the conspicuous proboscis structures of the Southeast Asian blood-sucking moths (BOURGOGNE 1970, NEMEC & KRENN, unpublished).

The enormous diversity of food sources used by neotropical butterflies contrasts with that of European butterflies. Compared to the hundreds of butterfly species in neotropical rainforests, a typical Central Eu-

ropean forest habitat contains only about 20 species (SBORDONI & FORSTIERO 1984). Of these, the great majority belong to the flower-visiting nectar-feeding guild and only exceptionally are there non-flower-visiting species which likewise are found primarily in forest habitats. An explanation for their near absence may lie in the seasonal restriction of ripe fruits to the late summer and autumn. However, this explanation is not entirely convincing, since flowers are also seasonally restricted in temperate habitats and mammalian faeces can be found in all seasons.

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